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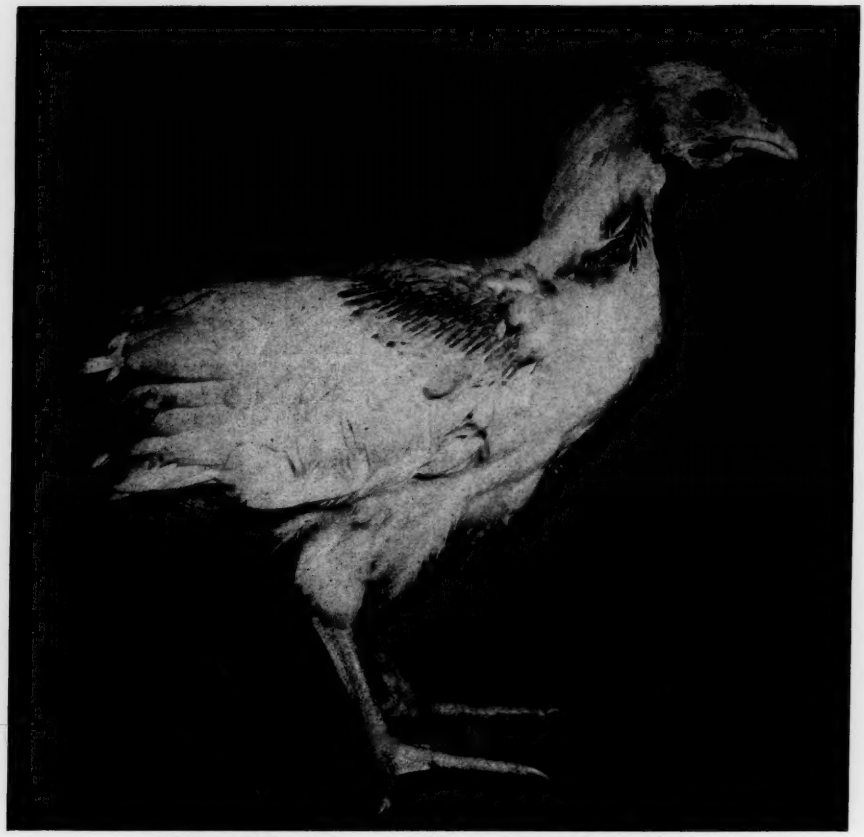

GROUNDED BY A SLOW-FEATHERING GENE

(SEE PAGE 203)

Yak Breeding in Asia

Wheat-Rye Hybrids

Swine Coat Color

VOLUME 37 JULY, 1946 NUMBER 7

The American Genetic Association

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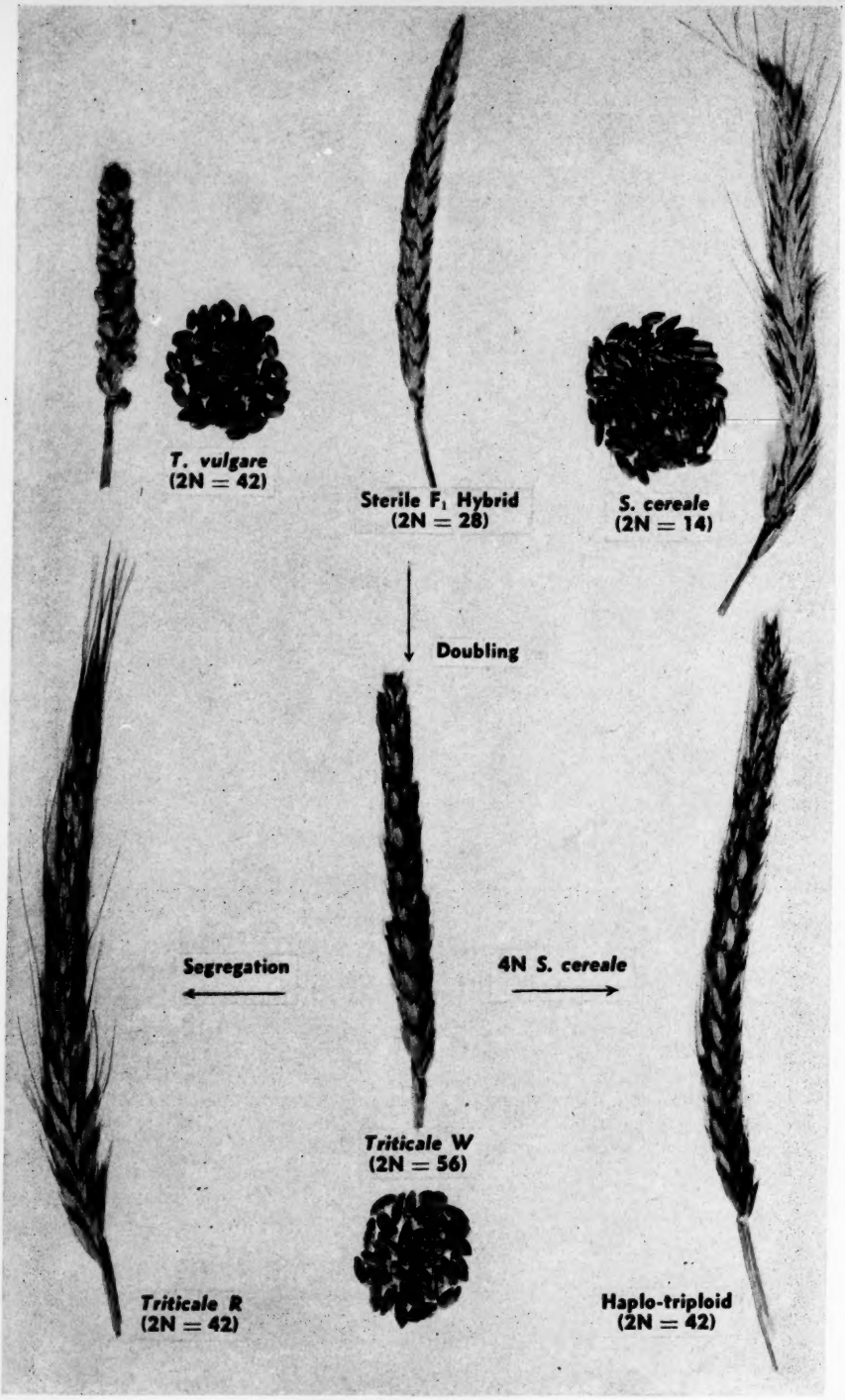

WHEAT-RYE HYBRIDS

Figure 1

When hexaploid 42-chromosome wheat is crossed with diploid rye, a sterile 28-chromosome hybrid is formed. When the chromosome number of this hybrid is doubled by treatment with colchicine a fertile 56-chromosome form is produced. From this are derived segregates ranging widely in predominance of wheat and of rye characteristics. Crossed with tetraploid rye a sterile haplo-triploid with 42-chromosomes is produced. The occasional chromosome doubling of sterile hybrids may have played an important part in the evolution of new forms both in nature and under domestication.

WHEAT-RYE HYBRIDS

T. C. CHIN

Arnold Arboretum, Harvard University

MANY attempts have been made to combine the desirable characters of wheat and rye, and a number of amphidiploid hybrids have been produced. Muntzing[4] has collected a number of these hybrids and crossed them *inter sē* and with wheat, but desirable types of economic value have not yet been obtained.

Hybrids between a variety of Chinese ($n = 21$) wheat and rye ($n = 7$) have been made at the Arnold Arboretum and have been made available to the author for cytological analysis. The F_1 shows few of the rye characters. Pollen sterility is complete and no seeds were obtained.

An amphidiploid hybrid was obtained by treating the F_1 seedlings with colchicine. The plants were relatively fertile although most of the grains were wrinkled, and viability was low even among the plump seeds. The progeny of the amphidiploid *Triticale* were relatively uniform, but differed considerably in fertility. Most of these plants resembled the F_1 but several had many characters of the rye parents.

The amphidiploid *Triticale* was backcrossed with $4n$ rye to obtain an equal number of wheat and rye chromosomes, which might lead to greater genetic balance. About 50 of these plants which were later proved to be seed infertile, were treated with colchicine to produce a new form of amphidiploid *Triticale*, but none has yet been produced. The parental species, the sterile and fertile F_1 hybrids, the rye-type segregate and the F_1 between *Triticale* and $4n$ rye are shown in Figure 1.

The original wheat-rye hybrid has 21 wheat and 7 rye chromosomes. At meiosis there are from 0-3 bivalents, often atypical, but most of the 28 chromosomes remained unpaired. Since bivalents occasionally occur in both haploid wheat and haploid rye the few bivalents found in this hybrid may involve pairing of intra-generic genoms.

In the amphidiploid, *Triticale* F_1, most of the chromosomes pair as bivalents, but with from 0-6 univalents (mean = 2.2). Presumably the 42 wheat chromosomes usually pair, while the 14 rye chromosomes form 7 bivalents, but some failure in pairing as well as atypical pairing does occur.

The wheat-like progeny of *Triticale* must have varying numbers of chromosomes due to irregularities in meiosis of the original amphidiploid. Muntzing has found forms with numbers ranging from 35 to 69. A cytological study of a typical segregate showing 56 chromosomes which at meiosis formed from 14 to 28 bivalents, 0-13 univalents, 0-4 trivalents and 0-3 associations of 4 chromosomes. The average number of bivalents was 21.7. In spite of such meiotic irregularity this plant was partially fertile.

The sterile rye-like segregate of our *Triticale* has $2n = 42$ chromosomes, the same as the original wheat parent, yet its more prominent rye characteristics, compared with *Triticale* $\times$ $4n$ rye, indicate the presence of more rye chromosomes. At meiosis there were an average of 8.0 bivalents, 13.7 univalents, 2.1 trivalents and 1.4 associations of four chromosomes.

In the backcross of *Triticale* F_1 $\times$ $4n$ rye there are presumably 21 rye chromosomes and 21 wheat chromosomes. At meiosis there were an average of 7.6 bivalents, 14.1 univalents, 2.9 trivalents and 1 association of four chromosomes. Since there is little pairing between wheat genoms most of the pairing must involve the rye chromosomes. But in this hybrid there are more bivalents than in the triploid rye described by Lamm[2] plus the pairing in haploid wheat described by Krishna-

swamy[1]. Some of this pairing must be attributed to pairing between wheat and rye chromosomes resulting from original or recent translocations and partial structural homologies.

There is considerable evidence of structural changes in the chromosomes of both types of segregates of *Triticale*. Unequal bivalents and chromatid bridges were found in both the wheat-like and rye-like segregates as well as in the back cross *Triticale* × 4*n* rye. The number of bridges at meiotic anaphase increases directly with the increased number of rye chromosomes present. There is also evidence of misdivision of the centromeres of the univalents in the second anaphase of *Triticale* × 4*n* rye.

The degree of pollen sterility varies directly with the numbers of chromatid bridges and varies inversely with the numbers of wheat chromosomes present in the hybrids. Thus, the rye-like segregate possessing (*N*-) wheat and (3*N*+) rye chromosomes, in combination with an average of 5.22 bridges per cell and a coefficient of hybridity of 0.2031, shows complete pollen sterility as a combined result of deficiency[6] and unbalanced segregation of chromosomes.[5]

The original amphidiploid F_1 and its wheat-like segregates are partially fertile but produce grains most of which are wrinkled and some badly shriveled. A study of mitosis in the endosperm tissue shows considerable mitotic irregularity. Occasional dicentric chromosomes are found, probably derived from broken bridges in meiosis perpetuated by the breakage fusion cycle[3]. In many cells the chromosomes are very short and resemble meiotic chromosomes in degree of spiralization and in orientation on the metaphase plate. These changes presumably are caused by lack of synchronization of chromosome and spindle development as the result of changes in genetic balance[7]. The spindles often are abnormal with double, tripolar and curved spindles. Occasionally the chromosomes simply degenerate into chromatic masses in the nucleus.

These mitotic abnormalities result in further loss of chromosomes and there is considerable variation in cell size and development. Such changes presumably are associated with poorly developed and wrinkled endosperms. Similar irregularities in the developing embryo may also account for the low viability of the seed of some of the *Triticale* types.

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Plans for Eighth World's Poultry Congress

The World's Poultry Science Association announces that plans are being formulated to hold the Eighth World's Poultry Congress. Congresses were held at three-year intervals between 1921 and 1939, the last at Cleveland. On May 4 a committee of the Assocation decided that 1948 would be the preferable year for the Eighth Congress, thereby retaining the three-year schedule with 1942 and 1945 having been skipped.

The host country will not be announced until sometime after December 31, 1946, in order to give interested countries time to submit their bids to the WPSA Secretary, Dr. G. F Heuser of Cornell University. Preference will be given to countries in which congresses have not been held.

The next congress will emphasize scientific sessions of experts, rather than exhibits with popular appeal such as the International Exposition at the Seventh Congress which drew an attendance of 850,000 people.

One objective of the Eighth Congress will be to appraise the position of the poultry industry in world food production.

MULTIPLE ALLELES AFFECTING FEATHERING IN THE FOWL*

D. G. JONES AND F. B. HUTT
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THE mating of related individuals often uncovers a recessive abnormality which might otherwise remain hidden for several generations because of the improbability that two unrelated or distantly related parents would both carry the same mutation. In this laboratory, some matings of related White Leghorns in 1940 brought to light a recessive mutation, hitherto undescribed, which causes unusually slow feathering in chicks homozygous for the mutant gene. Subsequent studies have shown that the mutation belongs to a set of multiple alleles. This is of some interest because in over 45 years of genetic study since the rediscovery of Mendel's laws, only one other series of multiple alleles has been found in the fowl. Details are reported in this paper.

The Three Alleles

The new mutation has been called "tardy" and assigned the symbol, t. It is somewhat similar to the "retarded" feathering described by Warren[6] to which it is recessive. Since no symbol has previously been used for Warren's retarded, we propose that it be labelled t^s. The superscript s is used as a reminder that the gene exerts its effect on the secondary flight feathers.

Both these mutations are recessive to the normal condition. In White Leghorns this is the type of rapid feathering which Serebrovsky[5] showed to be caused by a sex-linked gene. However, since the alleles considered in this paper are autosomal (as is shown later), it follows that the normal or wild-type member of the series, T, is merely a gene that permits full manifestation of rapid feathering in the manner usual with Leghorns. It is part of the genotype of all normal chicks with this type of rapid feathering.

Descriptions

Before giving the descriptions that follow, it should be made clear that all of them pertain to the effects of T, t^s, and t in rapid-feathering chicks only. We have made no studies of these genes in slow-feathering birds, but Warren's results with t^s led him to conclude that "it is difficult to follow the segregation of retarded in the presence of late feathering."

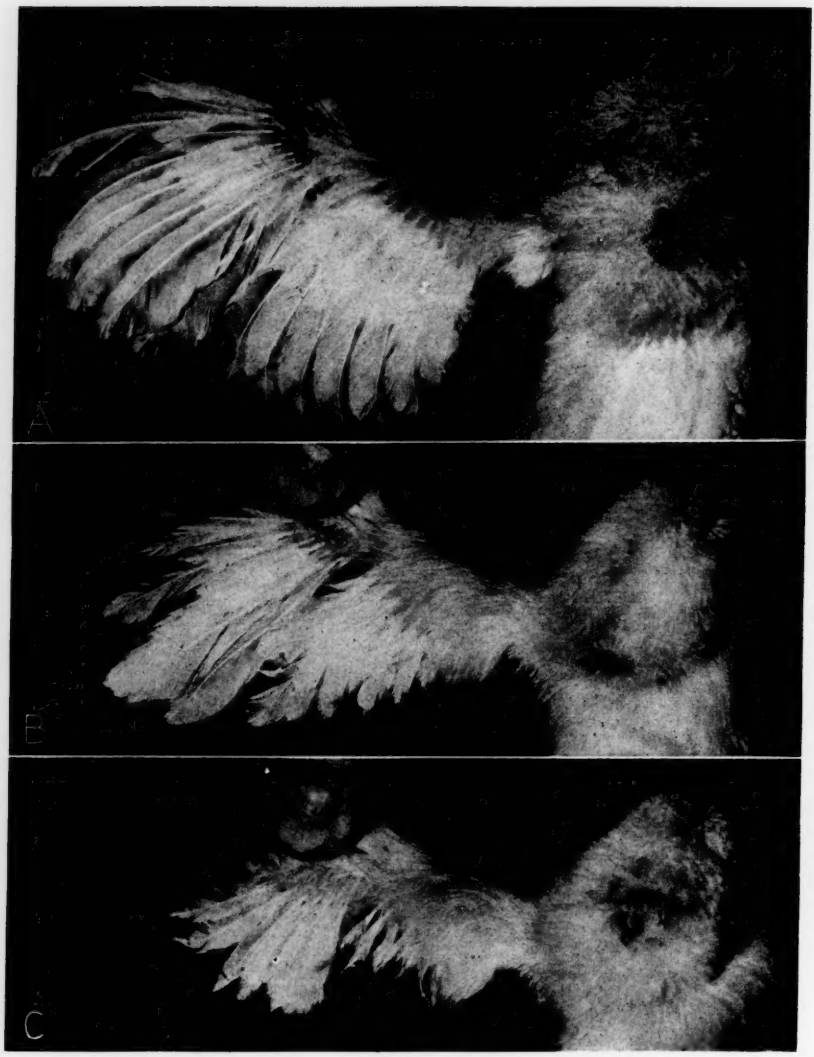
The descriptions of the mutant types apply equally well to both males and females as there is no difference in the expression of the abnormalities in the two sexes.

At hatching. In chicks, as in adults, the innermost primary feather is the first one to appear and later ones grow in succession distally (in the extended wing) to the first. Conversely, the outermost secondary is the first of that group and later ones appear in succession proximally to the first. The normal White Leghorn chick at the time of hatching has at least six primary feathers and an equal number of secondaries. These remiges show clearly on the under side of the wing, appearing somewhat like needles because of their retention within their sheaths.

In contrast, the retarded chick usually has only the first three secondaries well developed at hatching, while the primaries are approximately normal in number and development.

The tardy chick at this time has normal primaries but no secondaries. A few of them show almost normal devel-

* Number 21 in the series by F. B. H. entitled "Genetics of the Fowl."



THREE RATES OF FEATHER DEVELOPMENT

Figure 2

White Leghorn chicks, all ten days of age, showing the action of three alleles on development of the wing feathers. The chicks are homozygous for the three alleles: *A*—*TT*, conditioning normal wing development; *B*—the retarded allele $t^r t^r$, characterized by uneven remiges and no tail; and *C*—tardy (*tt*), the chick having no tail and no large secondaries. Growth and viability are apparently normal. Although no tails are shown here the presence of tail feathers in normal chicks and their absence in retarded and tardy chicks is readily apparent at this age.

opment of the first two or three secondaries at hatching.

At ten days. At this age the normal Leghorn chick has at least six well developed primaries, six secondaries of equal length and a small tail (Figure 2 A). The retarded chick has no sign of a tail and lacks the smooth appearance of the normal chick. This is because the remiges of the retarded chick are unequal in length. Only the first three or four primaries and secondaries are approximately normal in length, and thereafter each succeeding primary and secondary is successively shorter than the preceding one (Figure 2*B*).

In contrast, the tardy chick shows little or no development of the secondaries, and the primaries, while normal in number, are narrower and much shorter than those of the normal chick (Figure 2*C*).

At three weeks. At this age, normal chicks have many body feathers, a prominent tail, at least eight well developed primaries and eight secondaries (Figure 3*A*). Retarded chicks have a small tail, few body feathers, and only six primaries and six or more secondaries. Of these last, the first three equal the primaries in length (Figure 3*B*). Less difference is apparent between normal and retarded chicks at three weeks than at 10 days.

On the other hand, tardy chicks are more conspicious at three weeks because they have no tails (Figure 3*C*) and their secondaries are about 2.5 centimeters shorter than the primaries (Table 1). They show almost exactly the stage of feathering found in the retarded chick at ten days. The measurements taken at three weeks are the mean lengths for the first primary and first secondary, measured after being plucked. Although only ten retarded and seven tardy chicks were involved, statistical analyses showed that the tardy secondaries are shorter than both (a) tardy primaries and (b) retarded primaries and secondaries, by highly significant differences. This is perhaps even more evident in the illustrations of representative tardy and retarded chicks at this age (Figure 3).

At later ages. There is little change in the plumage of the normal chick at later ages, except that it becomes progressively smoother in appearance as more contour feathers are acquired (Figure 4). Similarly the retarded chick becomes normal by six weeks of age except for some irregularities of body plumage which cause a ragged appearance.

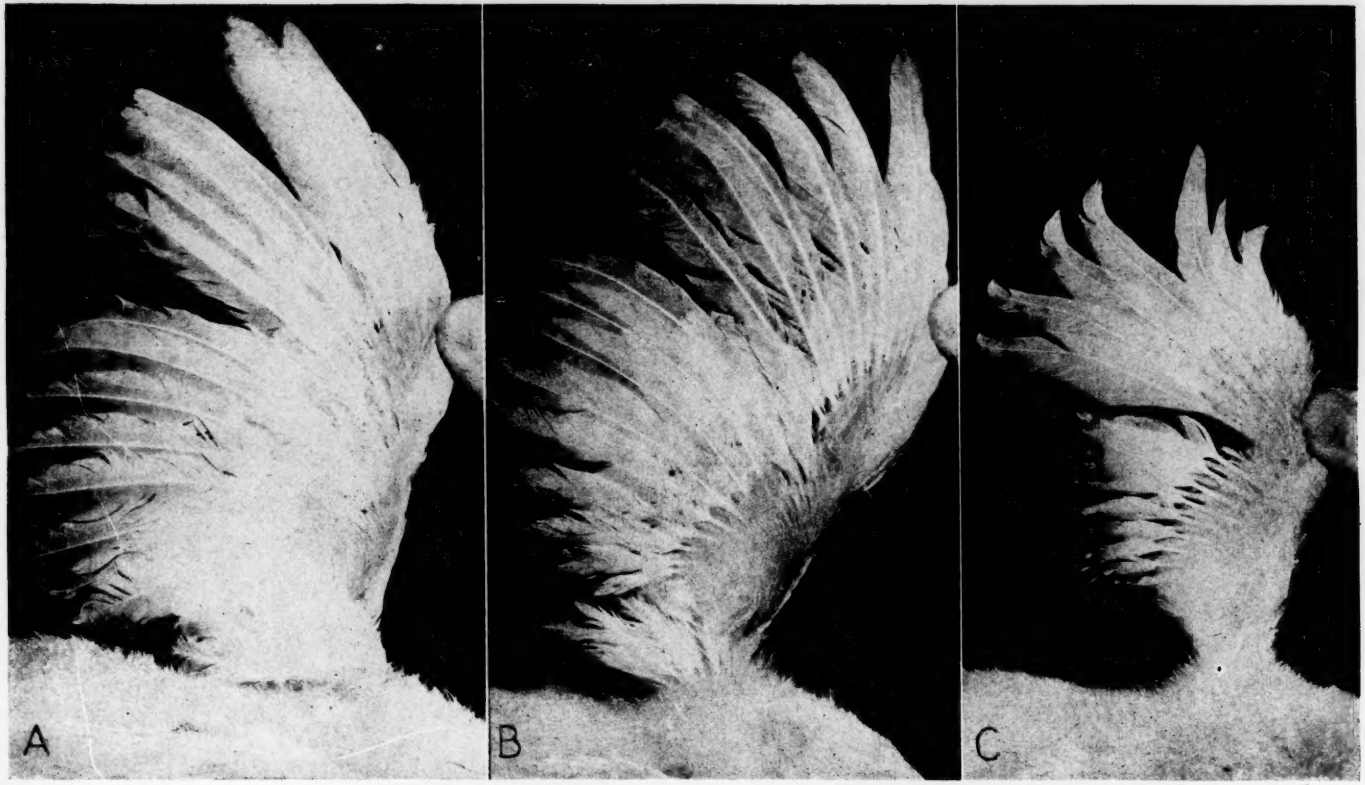
The tardy chick, however, continues to show its abnormally slow feather development for some weeks. Its tail feathers do not appear until at least eight weeks of age and even then they grow very slowly. Measurements at four and five weeks of feathers plucked from retarded and from tardy chicks (Table 1) showed that up to five weeks of age the secondaries of the tardy chicks were still 2.5 centimeters shorter than the primaries, this difference being high-

TABLE I. Mean lengths of feathers in retarded and tardy chicks.

Age—Weeks	Feathers	Retarded		Tardy		Difference
		cm.		cm.		
3	Primaries	8.72	(10)	8.50	(7)	+ .22
	Secondaries	8.30		5.99		+ 2.31 **
	Difference	+ .42		+ 2.51 **		
4	Primaries	9.88	(7)	10.08	(4)	— .20
	Secondaries	9.24		7.23		+ 2.01 **
	Difference	+ .64		+ 2.85 **		
5	Primaries	10.25	(4)	10.85	(4)	— .60
	Secondaries	10.53		8.35		+ 2.18 *
	Difference	— .28		+ 2.50 **		

** $p = <.01$ * $p = <.05$

Numbers in parentheses give the numbers of chicks in each class. Different chicks were used at each age.



WING-FEATHER DEVELOPMENT AT THREE WEEKS

Figure 3

Three-week-old White Leghorn chicks showing the effects of the alleles on development of wing feathers. *A*—normal (*TT*); *B*—retarded (t^rt^r); and *C*—tardy (*tt*). Retarded has begun to catch up with normal in development, though the tail feathers (not shown) are still small. Tardy shows extreme shortening of the secondaries, and the tail remains undeveloped (See Figure 5).

ly significant. (At these ages, the first three feathers of each kind were measured to determine averages for each chick, but the statistical analysis is based on the numbers of chicks as given.)

At maturity, retarded and tardy birds cannot be distinguished from each other, or from normal ones. Therefore birds showing the two mutant types of feathering should be eliminated from the potential breeding flock at an age when the type of feathering is still readily identifiable.

Classification

To determine the most satisfactory age for classification, chicks were examined at hatching, at ten days, and at three weeks. In matings which produced only normal and tardy chicks, classifications of over 200 chicks at hatching and at ten days agreed perfectly with but one exception, which was more likely an error in recording than one in classification. Classifications at ten days and at three weeks agreed perfectly. Similarly, Warren[6] found that normal and retarded chicks could be distinguished accurately at hatching time.

It is not easy, however, to differentiate between tardy and retarded chicks at hatching when both of these occur in the same population. Among 220 such chicks that were classified at hatching and again at ten days of age, 26 birds, or nearly 12 percent, were wrongly identified at hatching. Of these 26 chicks, all but three turned out to be tardy chicks mistakenly classified at first as retarded. This error is caused by the tardy chicks that show some development of the secondaries at hatching. Since these comprise about ten percent of all tardy chicks, the error entailed is too great to justify classifications at hatching when both tardy and retarded chicks are expected.

As the measurements in Table 1 show, tardy chicks may be easily distinguished from retarded ones (and also from normal Leghorns) up to five weeks of age. Even up to eight weeks they may be identified by their lack of tails and of feathers on the wing bow and neck (Figure 5). After that age, it is more difficult to recognize them. For that reason, breeders desiring to eliminate this undesirable mutation should identify their tardy chicks before the birds are eight weeks of age. Chicks with the mutation, retarded, are best eliminated at ten days of age.

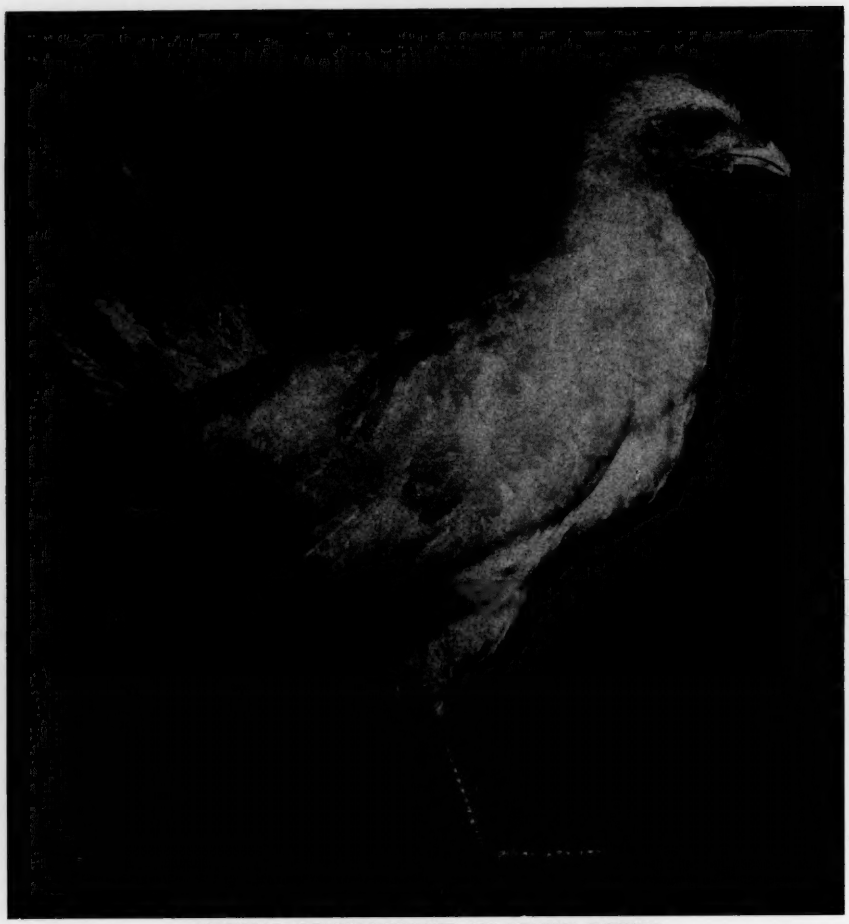
Genetics

A—Analyses of tardy

Results below show tardy, *t*, as a simple autosomal mutation, recessive to the normal rapid feathering, *T*, of Leghorns.

Mating	Offspring Normal	Tardy
I a Normal ♂ × tardy ♀♀	21	0
I b Tardy ♂ × normal ♀♀		
(1) ♂ H 5072	34	0
(2) ♂ H 5074	47	0
	102	0
II F_1 ♀♀ backcrossed to tardy ♂♂		
(1) to ♂ H 5072	24	33
(2) to ♂ H 5074	14	11
(3) to ♂ H 5075	3	1
	41	45
III a F_1 ♀♀ backcrossed to normal ♂♂	93	0
III b F_1 ♂♂ backcrossed to normal ♀♀	175	0
	268	0
IV F_1 ♂♂ × F_1 ♀♀ to yield F_2 generation		
(1) ♂ E 5806	108	39
(2) ♂ H 5149	17	7
	125	46
V Tardy ♂♂ × tardy ♀♀		
(1) ♂ H 5071	0	10
(2) ♂ H 5072	0	48
(3) ♂ H 5074	0	27
	0	85

The fact that reciprocal matings between normal and tardy (Ia and Ib) yielded only normal chicks is ample evidence that this new mutation is not sex-linked. The observed F_2 ratio of 125 : 46 fits closely to the expectation of 128.25:42.75 ($\chi^2 = 0.3295$, $p = .50$-$.70$). It should be noted that two tardy males, H 5072 and H 5074, were both used in three different types of mating, yielding successively (Ib) only normal chicks, (II) a ratio of 1:1, and (V)



NORMAL DEVELOPMENT AT EIGHT WEEKS

Figure 4

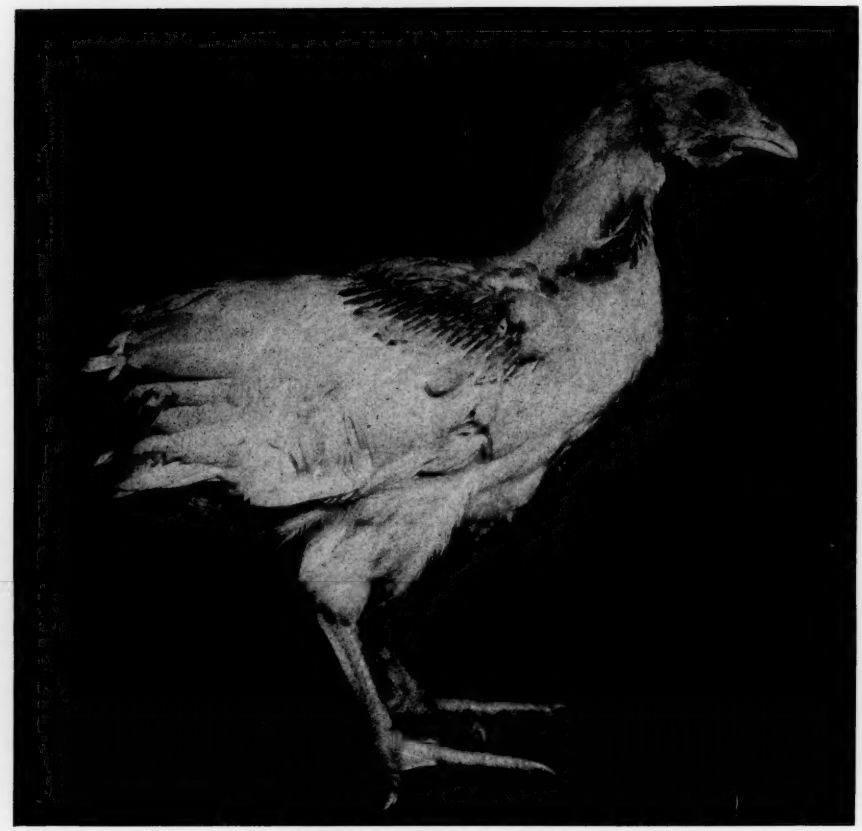
White Leghorn cockerel at eight weeks of age, showing well developed feathering. Before they reach this age, normal Leghorn chicks are capable of flight for short distances.

only tardy chicks. The result in each case was that expected for males of the genotype *tt*.

B—Evidence that tardy and retarded are alleles

The differences between tardy and Warren's "retarded" mutation, described earlier in this paper, were not so obvious until the former character had been studied for some time. The similarity of the two suggested that they might be caused by the same gene, and that the more noticeable differences might be attributed to the action of different modifying genes in the two stocks. To test this point, Dr. Warren kindly furnished a retarded male for breeding tests.

In 1942 this retarded male was mated



TARDY IS STILL A "KIWI"

Figure 5

At eight weeks of age homozygous tardy Leghorns (*tt*) have no tail and only rudimentary secondary wing feathers. They are still grounded by their delayed feather development. Note that the plumage of the wing bow and the neck is also deficient. Eventually these birds attain a complete set of feathers.

with tardy females. If the two types of feathering were caused by two different recessive mutations, only normal chicks were to be expected from this mating unless there were some interaction of the two genes. Somewhat to our surprise, every chick—41 in all—showed the retarded type of feathering, and none could be classified as tardy. This suggested that three alleles were involved, with retarded (t^s) dominant over tardy (t) and both of these recessive to normal (T). A further test of this hypothesis was made in 1943 with reciprocal matings between t^st and tt birds. These yielded 220 chicks that lived till ten days old or longer. Those dying before that age were not counted because of the difficulty of distinguishing with accuracy between retarded and tardy chicks at hatching. When the 220 were classified at ten days of age and again at three weeks, the ratio of retarded to tardy (Table 2, Mating 2) was very close to that of 1:1 expected ($\chi^2 = .6546$, $p = .30\text{-}.50$).

The critical evidence that three alleles were involved was provided by the mating, *Tt* female × $t^s t$ male. The expectation here was 2 normal : 1 retarded : 1 tardy. Only a single *Tt* hen was available for this mating and only twelve chicks were produced. However all three types of feathering did appear, and in about the expected proportions (Table 2, Mating 3). This could not have happened unless *T*, t^s and *t* were alleles.

C—Distribution of the mutation

Chicks with abnormal feathering are occasionally found in Leghorn flocks, where, made conspicuous by their lack of tails, they are usually considered as "runts." It seems probable that some of these chicks may merely be showing the tardy or retarded mutations.

In 1941, one of them was sent in to this laboratory from a flock of White Leghorns 40 miles away that, so far as is known, was quite unrelated to the local stock. At three weeks of age this chick was indistinguishable from our tardy chicks of the same age. It was reared to maturity, at which time appropriate breeding tests were made. Fortunately it was a male. Tests with *tt*, *Tt* and $t^s t$ females proved that it was homozygous for the mutation, *t*.

Another chick, phenotypically indistinguishable from the tardy mutants illustrated in this report was found in 1946 among chicks from a prominent breeder of White Leghorns in New York State.

Since these studies were begun, McClary and Bearse[3] have briefly reported a recessive autosomal mutation causing slow feathering in White Leghorn chicks in the State of Washington. From the meagre description given, it is difficult to say whether or not this is the same as the tardy mutant described in this paper.

Discussion

From the standpoint of the poultry breeder, it would seem desirable to eliminate the t^s and *t* genes from any flock of purebred Leghorns. Both retarded and tardy chicks appear to be unthrifty because of their ragged plumage. This condition lasts only a short time in the retarded chicks, but for eight weeks or more in the tardy ones. Defective plumage at these later ages may reflect adversely in the market value of the birds as broilers.

Apart from this, the mutations are important because of the present trend in poultry breeding to avoid the undesirable "barebacks" at broiler age in Rhode Island Reds, Plymouth Rocks and other heavy breeds by making them rapid-feathering instead of slow-feathering. This is done by replacing the sex-linked gene, *K*, for slow feathering with its allele, *k*, which causes rapid feathering of the Leghorn type. The studies reviewed in this paper show that the type of rapid feathering sought depends upon both sex-linked and autosomal genes. So far as is now known the desired genotypes are *kk TT* for males and *k* — *TT* for females.

Other genes are undoubtedly involved. By selection, Hays and Sanford[1], and Radi and Warren[4] increased the amount of feathering on the back at seven or eight weeks in Rhode Island Reds. Hays found that chicks of this breed could show the sex-linked rapid feathering at ten or 12 days but be quite bare on the back at eight weeks. He considered that such birds lacked a dominant autosomal

TABLE II. Matings showing that *T*, t^s and *t* are alleles.

Type of Mating		Progeny		
		Normal	Retarded	Tardy
1. Retarded × tardy, both homozygous $t^s t^s$ × *tt*	Observed	0	41	0
	Expected	0	41	0
2. Heterozygous retarded × tardy $t^s t$ × *tt*	Observed	0	104	116
	Expected	0	110	110
3. Normal × retarded, both heterozygous *Tt* × $t^s t$	Observed	7	4	1
	Expected	6	3	3

gene necessary for good back feathering. It seems unlikely that this could be the same as the gene, *T*, because *tt* chicks could not have been recognized at ten days as having rapid feathering.

For geneticists the genes, *T*, t^s and *t*, have some interest because they comprise the second series of multiple alleles to be identified in the fowl. The first such case was the set of three genes found by Warren[7] to cause polydactyly, duplication or normal development of the first digit on the foot.

Another point worth noting is the variation in time at which genes affecting feathering exert their effects. Considering only the remiges and rectrices, the visible effects of t^s (when homozygous) are restricted to the first six weeks, those of *t* to the first eight weeks of life. Neither gene has any noticeable effect on the adult plumage which, in Leghorns, begins to replace that of the chick at about six weeks of age. Conversely, there is a mutation, ragged wing, which Hutt, Mueller and Warren[2] found to eliminate or shorten some or all of the definitive remiges of the adult, but which has no visible effect whatever on those of chicks.

Summary

A mutation, tardy, in White Leghorns was found to prevent manifestation of the sex-linked type of rapid feathering characteristic of chicks of that breed. It causes slow development of the tail, of secondary feathers of the wing, and of contour feathers over the body. It is recognizable between ten days and eight weeks of age, and has no effect on the plumage of adult birds.

This condition is caused by a recessive autosomal gene, *t*, when homozygous. By suitable breeding tests, it was found that tardy is a recessive allele of the mutation, retarded, previously reported by Warren, to which the symbol t^s is now assigned. These two genes with their dominant, wild-type allele, *T*, thus comprise a series of multiple alleles. This is the second such series to be identified in the fowl.

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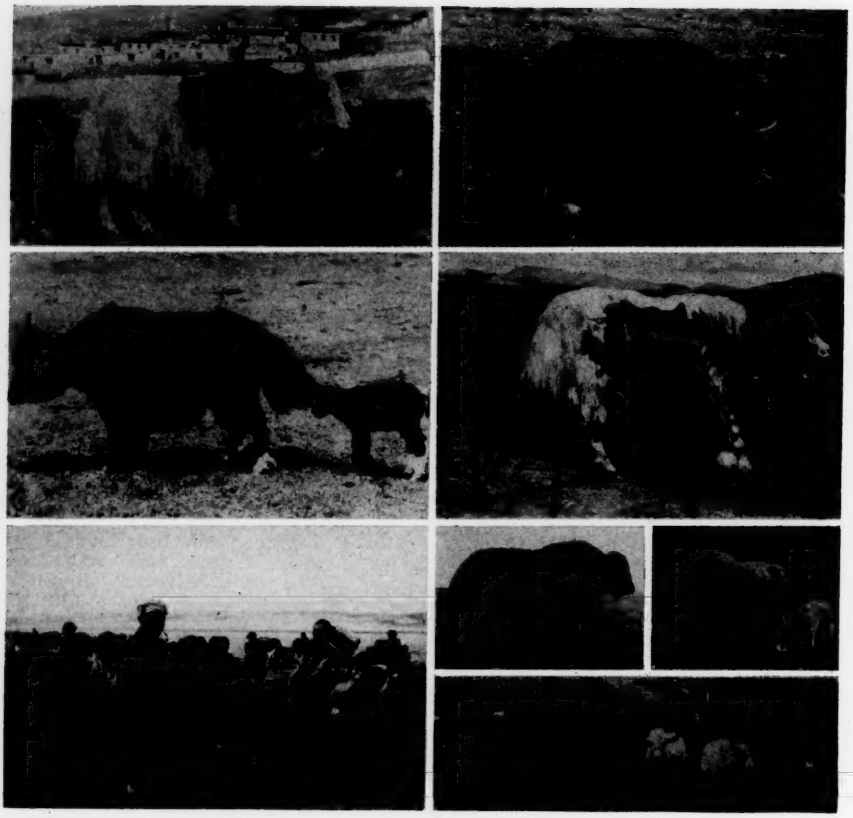
Biological Photographers to Meet in Chicago

The Biological Photographic Association will hold its sixteenth annual meeting at the Hotel Bismarck in Chicago, September 6, 7, and 8. The planning and production of teaching motion-picture films will be discussed by experts. New equipment for both still and motion picture photography will be demonstrated. Discussions will be held on the preparation of scientific exhibits; the classification, indexing and filing of medical illustrative material, and The Veterans Administration's program for obtaining medical illustration material will be described. Practical papers on fundamental technics will be presented; as well as more specialized work on endoscopic photography, photomicrography, etc. Photographs by many of the leading biological photographers will be seen in the Annual Salon; and new materials and equipment will be shown in the Technical Exhibit. Jay Garner, M.D., of Winnetka, Ill., is Convention Chairman. Ralph Creer, of the Motion Picture Committee, American Medical Association, is in charge of the program.

The Biological Photographic Association, a non-profit organization, was formed in 1931 to raise the standards in photography for teaching and research; and to act as a clearing-house for information on photographic methods. Its members are professional scientific photographers, scientists with an interest in photography as applied to their fields; and designers of precision equipment. The association's Journal is published quarterly. It constitutes a volume of about 250 pages, which is furnished free to members. Further information about the Association may be obtained by writing the Secretary of the Biological Photographic Association, University Office, Magee Hospital, Pittsburgh 13, Pa.



YAKS OF THE TIBETAN HIGHLANDS

Figure 6

A—Yak bull belonging to a lamasary in Lihua, Sikong. *B*—a young cow in Sikong, still in full winter coat. *C*—Yak cow and calf in Sikong. *D*—Yak cow in Chinghai. *E*—A large yak, measuring 5 feet, 2 inches high at the withers. *F*—Yak bull in Chinghai. (Photo by S. F. Wu, Northwestern Agricultural College, China. *G*—A white yak bull in Chinghai. (Photo by E. A. Tunnicliff, Montana State College). *H*—A group of animals showing mixtures of yak and cattle blood. The white bull in the center appears to be predominantly of yak blood, while the others show evidence of varying degrees of cattle blood.

YAKS AND YAK-CATTLE HYBRIDS IN ASIA

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The first part of this paper appeared last month.

Yaks and Yak-cattle hybrids are the most important livestock kept by the Tibetans. Well adapted to foraging and working at high altitudes, they are used extensively for packing. By-products are milk, butter, hair (woven into cloth for making tents), and chips for fuel. The hybrids, called *pien niu* by the Chinese, are usually, but not always, produced by mating "yellow" bulls to yak cows. Male hybrids are sterile, females are fertile. Hybrids are larger, can carry heavier loads, produce a little more milk and have less stamina than yaks.

Breeding Problems

NO data are available on the age of puberty, duration of estrus, the estrous cycle, and pregnancy in the Tibetan yak and *pien niu*. One worker[9] who managed a large herd of *pien niu* in a dairy stated that the estrous cycle was about 21 days in length and pregnancy lasted about nine months, the same as in domestic cattle.

Breeding efficiency is apparently low, although no accurate data are available. In Sikong, for example, it is estimated that not more than 50 per cent of the yak females of breeding age produce calves in any one year.

There is no organized system of breeding in most areas. Bulls usually run with the females of all ages throughout the year, hence neither the time of calving nor the type of mating can be controlled. In addition to the bulls that run with owners' herds, there are many herds of "liberated bulls" that roam about at will. These are bulls that have been donated "to Budda and nature," and it is not uncommon to see a herd of 15 or 20 of them roaming about. In the wild state, the time of breeding is reported to be during July and August when the grasses are best, but no accurate data are available. The yak is said to come in estrus about a month earlier in the summer than the *pien niu*.

Little selection of breeding stock is practiced. The females in the breeding herd are those that are able to survive the rigorous environment. Selection of a male for breeding may be merely a matter of chance or be based on the owner's preference for some color or other trait. The woman of the family frequently makes the selection of a male to be saved for breeding, and there is one herd near Tai Ning, Sikong, in which most of the animals have white faces, owing to the preference of the wife of the owner for white faces and the continuous selection of white-faced animals for breeding.

Due to the lack of a systematic breeding program, the breeding of yaks and *pien niu* is in a chaotic condition. *Pien niu* are usually produced by mating yellow bulls to yak females, but offspring from the reciprocal cross are also called *pien niu*. Hybrids from the two methods of crossing are said to differ in certain characteristics. It is claimed, for example, that hybrids from yellow-cow dams have smaller tails and louder voices than those from yak dams. The latter type are said to have tails more like those of the yak and to have longer hair, quieter disposition, and greater prolificacy. Whether these beliefs have any basis in fact remains to be determined. It seems probable that many of them are folklore that may not stand up under critical tests.

Terminology for describing the various crosses is confused. In some areas the progeny of a cross between the *pien niu* female and either the yak or yellow bull is referred to as a *galiba*, while the Tibetans refer to these as *ah gohr*. In other areas only the progeny resulting

from mating yak bulls to *pien niu* females are referred to as *galiba*. This latter cross is the one most frequently made. After a few crosses back to either yak or yellow bulls (three in some areas) the offspring are referred to as yaks or yellow cattle, according to the type with which the hybrids were backcrossed.

The *pien niu* males are reported to be sterile, and the same is claimed for males resulting from backcrosses either to the yak or yellow cattle. This belief is widespread in the areas where *pien niu* are produced. Lus[16] made the same claim concerning *pien niu* in outer Mongolia. These field observations are supported by the work of Zawadowsky[22] and Zuitin[23]. Zawadowsky reports that male hybrids between yak and zebu cattle, and backcross males were sterile in the Moscow Zoological Park. Histological study of the testes revealed that interstitial tissue was well developed but no spermatozoa were produced. Zuitin observed testes of two yak bulls, one hybrid with Kirghizian cattle and one quarterblood yak. No differences were found in interstitial tissue and Sertoli cells. Seminiferous tubules were smaller in the hybrid than in the yak, and those of the hybrid had little germinal tissue. Spermatogenesis had proceded further in the quarter-blood yak, but ceased after primary spermatocytes were formed. Zuitin and Ivanova[26] confirm these observations and report an additional case, a ¾ yak, in which mature spermatozoa were found in a few isolated regions of the testes but their motility and fertilizing capacity were not established.

Ivanova[10] examined the ejaculate of F_1 males and found no spermatozoa. A few normal or motile spermatozoa were found in the semen of backcrosses to either parent, but as a rule the spermatozoa were either abnormal and dead, or very scarce and dead. A ⅞ domestic bull was found to have entirely normal sperm with few defective types, and he sired progeny. Ljubimov[14] also observed that ⅞ domestic bulls were fertile.

Female hybrids are fertile, and no difficulties were reported in the Tibetan area in utilizing them for breeding, so far as fertility is concerned. This is borne out by observations of Lus[16] in Outer Mongolia,, and by Vlasov, Gershenzon and Poliakov,[21] who studied hybrids between yak and cattle in the Oirat District of the U.S.S.R. Druzinin[7] reports that the pituitary gland of the yak is less developed than that of cattle, and that the absolute and relative weights of the ovary are lower than those of cattle, sheep and goats.

The situation regarding fertility is similar to that observed in American bison and cattle hybrids. The bison is probably the closest living relative of the yak. In the Canadian work, reported by Deakin, Smith and MacLellan,[3] no hybrid males, or males resulting from succeeding backcrosses to domestic cattle, were fertile except a $^{31}/_{32}$ domestic bull. Since that report was published, Deakin[1] reports that one fertile ¾ domestic-¼ bison was obtained.

The yak male appears to have smaller testes than "yellow" bulls and they are contained in a smaller, tighter scrotum. The bison male also has a small, nonpendulous scrotum which holds the testes close to the body. In sheep (Phillips and McKenzie[19]) and in cattle (Lagerlof[13]), as well as some laboratory animals, it has been demonstrated that the scrotum serves a thermo-regulatory function, keeping the testes cooler than the body cavity, and raising of the testicular temperature results in sterility. Deakin, Muir and Smith[2] state that the scrotal form of the bison is partially dominant in first-cross hybrids, while ¼ bison animals show some variation. They suggest that the hybrids are sterile owing to a higher scrotal temperature than the hybrid testes can withstand. This view is supported by the cryptorchidlike appearance of seminferous tubules in the ½ and ¼ bison males slaughtered. The same situation may hold in yak-cattle hybrids.

Male *pien niu* and backcrosses are usually castrated in the Tibetan area. There is a strong superstition among

YAK AND *PIEN NIU* CARRY THE FREIGHT IN TIBET

Figure 7

A—Loaded yak plowing through snow on the uplands of Tibet. *B*—Part of a loaded pack caravan in Sikong. *C*—Loaded animals climbing a steep grade. *D*—A large caravan being prepared for the night at Kangting, Sikong.

Tibetans against mating *pien niu* with either yak or cattle or among themselves. They also believe that the progeny of females of such crosses are generally inferior. This latter belief was also prevalent among Mongolians who raised yak and *pien niu* in the Kansu corridor area. Lus[16] who studied yak and yak-cattle hybrids in Mongolia found some evidence of heterosis in the first backcross to either parent, but states that later generations of hybrids are considered to be quite unproductive and are eliminated.

Zuitin[24] studied the number of chromosomes in the yak, in spermatogonial plates, and concluded that the diploid number probably is 64, and states that in general appearance the chromosomes resemble those of cattle. In a later report based on more material, Zuitin[25] indicates that the number is 60. This latter figure corresponds with the estimate of 60 chromosomes in cattle, reported by Krallinger, and quoted by Lush.[17]

New-born calves are usually segregated from their dams, or housed in the Tibetan families' yak-hair tent at night, for safety, and also to reserve all or most of the morning milk for human use. Calves then follow their dams during the day unless the weather is too stormy. At night the milk not nursed by the calf is taken for human use. In some areas animals are milked only once daily, usually in the morning.

The practice of allowing the calf to suck just enough to stimulate the letting-down of milk is almost universal among

nomads. It appears to be essential with yaks, but many *pien niu* will apparently let down their milk without this stimulation. With some females, it is necessary to allow the calf to suckle several times during the milking process to obtain all the milk. Skins of dead calves are sometimes stuffed with straw and placed before the females at milking time to help stimulate the milk flow.

The Tibetans usually milk with the hands wet. Dry-hand milking apparently has not been practiced in this area. The front legs, and also the rear legs, are usually tied together while yaks and *pien niu* are being milked.

Concentrates are seldom used in feeding calves. Some whey left from the making of casein or "milk residue" is occasionally fed. Calves learn to eat grass when quite young. During the summer months when grass is growing the calves make fair growth, but during other portions of the year, and especially during the late winter and spring months, there is not enough feed to permit normal growth. These periods of near-starvation stunt the young stock and weaken mature animals. Losses are heavy. It is especially difficult for the calves and yearlings to "drag through" the winter.

Observations on Yaks and Yak-Cattle Hybrids in Mongolia and Russia

Zawadowsky[22] states that hybrids between yaks and zebu cattle in the Moscow Zoological Park were larger than either parent.

Lus[16] who studied the yaks of Outer Mongolia reports the average height to be 109 cm. He found that about 20 percent of the yaks were of solid color, and that the remainder showed varying degrees of white marking, ending in practically pure white with a few colored specks. A type of roaning which gives the animal a blue tint was observed in 21.5 percent of the cases. Two types of white markings were described. In one the white is limited to the head, tail, feet and inguinal region. In the other, the color-sided type of piebaldness is found. The milk yield of the yak was reported to be low, but the fat content was about 6.34 percent. It is stated that there were 449,600 yaks and 40,700 yak-cattle hybrids in Outer Mongolia in 1930. He found no marked differences between yaks of Mongolia and those of Kirghizstan and Oirotio, except that there was a higher proportion of polled animals in Mongolia, owing to a preference for this type. All bulls observed in service in Mongolia were polled and 88.5 percent of the females were also polled.

The yaks of the Altai Mountains were studied by Denisov and Usakov,[6] who found that they did not differ materially from the Mongolian yaks described by Lus.[16] They state that the domestic yak yields a rather small carcass of poor-quality meat, and that the milk yield is low, with an average fat content of 6.34 percent. F_1 hybrids were reported to exhibit a marked degree of heterosis, giving larger carcasses of better quality beef and a higher milk yield. Fat percentage in the milk of hybrids was intermediate to the parent types.

Vlasov, Gershenzon and Poliakov[21] studied the yaks and yak-catttle hybrids in the Oirat District of U.S.S.R. They state that there were about 6,800 yaks in this area, and about 570 hybrids which were produced by natural interbreeding among yaks and cattle which grazed together. The musculature of the hybrids was well developed in all parts of the animal used for meat. Hybrids weighed 335 kg. on the average at six years of age, while local yaks and cattle averaged 231 and 200 kg., respectively. The slaughter or carcass yield of hybrids was 52.5 percent of live weight, as compared with about 40 percent for the native yaks and cattle. The meat and hides of the hybrids were equal to those of the cattle and superior to those of the yaks. The coat of the hybrids had no commercial value. Milk production was not studied specifically, but the available data indicated that in both quantity and butter-fat content it was intermediate, in the hybrids, to the parent types.

Gitz[8] reports on the hybridization of Swiss bulls and yak cows in Kirghizstan, and states that the results were very satisfactory. The hybrids were large,

well-proportioned, and measurements were intermediate or approached the larger parent. Gitz also states that hybrids between yaks and local cattle are very popular in this area.

Ljubimov[14] reports that hybrids between yaks and native cattle at the Oirat experiment station surpassed both the parent types in live weight, milk yield, and carcass yield. Triple-cross animals produced by mating hybrid females to Simmenthal bulls had excellent conformation and approached the Simmenthal in most measurements.

Kozarin[11] reports on three years of work with yaks and yak-cattle hybrids at an elevation of 225 meters. He states that the yaks fared badly at this altitude. Cows weighed only 233 kg. as compared with 277 kg. in their native habitat at about 2,000 meter elevation. New-born calves weighed 13.2 kg. and gained only 0.23 kg. daily, the slow growth being attributed to poor milking capacity of the yak cows. Hybrids showed definite signs of heterosis, weighing 326 kg. as compared with 246 kg. for Altai cattle and 233 kg. for yaks. It is stated that they thrive well and produce much more milk than the yak, with yields of up to eight liters per day, and with a fat content of up to 7.5 percent. Carcass yields or dressing percentages of hybrids averaged 47.1 percent, compared with 42.8 and 41.6, respectively, in yaks and Altai cattle. The carcasses of the hybrids had 13.8 percent of bone which the authors stated is a very low percentage.

Denisov[4] reports observations at a number of state farms in Kirghizstan. Breeding methods were primitive and the yaks were on pasture throughout the year. Animals were first bred at two years of age. Males were retained until eight of nine years old and females until 15 or 16 years. The breeding season is in July and August, and it is stated that yaks appear to be polyestrous. The yak is described as being small, measuring 109.2 cm. at the withers, and having a strong skeleton and a deep chest. The average weight of adult animals was 279.5 kg. The prevalent color is black with or without spotting, and other colors are rare. The winter coat consists of downy, medium, and coarse hair. The summer coat contains no down. The coats of calves are most valuable since they contain more and longer down. Yearlings yield 0.82-0.84 kg. of coat, while older animals yield 0.57-0.61 kg. of finer coat and 0.75-1.35 kg. of hair. The average milk yield during 225 days of lactation was 650.4 liters, with 6.7 percent butterfat. The highest daily yield recorded was 6 liters. Comparison of animals from different areas indicated that the Chinese and Kirghizstan yaks are identical, while those of Altai and Mongolia are slightly inferior.

Denisov[4] also reports on hybrids between the yak and Kirghiz, and also Brown Swiss cattle. He states that natives usually mate yak bulls to Kirghiz cows, but that the reciprocal cross is possible, as shown by successful matings of Brown Swiss bulls to yak cows. All the absolute body measurements of Brown Swiss × yak hybrids were superior to those of the parental types except live weight. The respective weights of Brown Swiss cattle, yaks and hybrids were 346.0, 178.6, and 312.7 kgs. At birth the hybrids were almost exactly intermediate in weight, and their relatively greater subsequent development was considered an indication of heterosis. Data on milk production in hybrid cows were quite limited. A representative animal yielded 894 liters of milk testing 4.4 percent fat in 230 days, and it appears that the average yield is greater than that of the yak, and the fat percentage was higher than in Kirghiz cattle. It is concluded that the yak is a valuable animal, that many of its characteristics can be improved by selection, and that it is well adapted for mating with Kirghiz cattle to produce utility animals.

Denisov[5] reports a number of interesting observations on yaks and yak-cattle hybrids. He points out that in Kazakhstan only nine to twelve percent of the yak population are hybrids with native cattle, even though the yaks and cattle are herded together. He believes that this is due to preferential mating, and to the short breeding season of the yak.

DOMESTICATED AND WILD YAK COMPARED

Figure 8

The domestic yak (left) does not reach as great a mature size as the wild yak, as is evident by comparison with the skull of a wild yak (right).

It was found that Swiss × yak hybrid females bred at 15 to 20 months compared with 24 to 30 months for yak females. Hybrid cows came in estrus during the winter, but their main breeding season was similar to that of the yak, June to August. Gestation in the yak averaged 258 days and in Swiss cattle 287.57 days. In Swiss × yak matings the average gestation period was 276.2 days. In backcrosses of the hybrid females to Swiss and yak bulls the respective gestations were 282.35 and 265 days. The hybrids were more resistant to hard winter conditions than native cattle, the respective losses in weight of yak, Swiss × yak hybrids and Kirghiz cattle being 16.8, 19.0 and 27.5 percent. Duration of lactation in Swiss × yak hybrids was 286.3 days, or 30 days more than in yaks, and average milk yields for the hybrids and yaks were 2021.5 kg. and 607.9 kg., respectively. Kirghiz cows yielded 1155 kg. of milk and Kirghiz × yak hybrids yielded 1124.4. The fat content in hybrids was approximately intermediate to the parent types.

In an attempt to determine the basic cause of heterosis in hybrids, Kushner[12] studied the blood of 215 animals, including yaks, Simmenthal grades and their hybrids. He determined hemoglobin content, number and size of erythrocytes, and alkalinity of the blood, and found a positive relationship between these values and body weight. Hybrids were significantly higher than the parent types and it was suggested that better oxidizing capacity of the blood may

account for the greater growth of hybrids.

Inheritance of Various Traits in Yak-Cattle Crosses

Several workers[2,4,8,11,21,22] have observed the characteristics of hybrids at various places. There is general agreement in their findings among themselves and with the observations of the authors. These are summarized below.

In general conformation, the hybrids are intermediate to the parental types, but there appears to be a tendency for cattle characteristics to predominate in the fore quarters and yak characteristics to predominate in the rear quarters. The low back of the yak also appears to predominate in the hybrid. Zawadowsky[22] found that the long body of the yak is dominant over the square body form of the zebu, while Denisov[4] found that the hybrid inherited the short body of the yak rather than the longer body of Kirghiz cattle. Differences in type of yaks, or in the cattle species used, or both may be responsible for this apparent inconsistency.

The coat of the hybrid is shorter and finer than that of the yak and has hardly any down or fine undercoat.

The absence of hair fringe appears to be dominant or partially dominant, since the hybrids usually do not have a definite fringe, but usually have more hair on the flanks, thighs and chest than cattle. A few fringe hairs may be present. Vlasov, Gershenzon and Poliakov,[21] state that the degree of hairiness varies, approaching one or the other of the parental types. However, their observations were made on hybrids in a mixed herd of yaks, cattle and hybrids under natural mating conditions and some of the hybrids may have had a preponderance of yak or cattle blood.

The long hair of the yak tail appears to be dominant or nearly so, since most hybrids have a tail very similar to that of the yak.

The voice of the hybrid is intermediate between the grunt of the yak and the low of cattle.

Horn shape in the hybrids is generally intermediate to the parental types.

Kozarin[11] states that yaks have few sebaceous glands in the skin, and that when soaked with water the coat dries out slowly, while hybrids have many sebaceous glands.

Color inheritance is quite varied, since there is some variation in the color of yaks used and considerable variation in the color of cattle used in crosses. Zawadowsky[22] found that the black-brown of the yak was dominant over the gray of the zebu cattle used in his crosses. Gitz[8] states that hybrids between Brown Swiss cattle and yaks had the color of the Swiss cattle. Denisov[4] states that the color in hybrids was quite varied and that it may be of the yak type, intermediate, or more rarely of the domestic cattle type. Deakin, Muir and Smith[2] report on several crosses involving Aberdeen Angus, Hereford or Shorthorn cattle and yaks. Two matings of Angus sire × yak dam gave two black offspring. Matings of a yak sire to two Hereford cows gave one dark brindled with white face, breast, and udder, and one brindled with white rear feet and a star. When an Angus was mated to two hybrid Herefords, four hybrid Angus and two hybrid horn cows, the resulting eight progeny were all black.

Wild Yaks

There are no longer any large herds of wild yaks in Tibet and smaller groups are found only in isolated areas away from caravan trails. Introduction of the automatic rifle has contributed largely to the depletion of the original herds. No game laws are in existence which protect them. One of the authors (I.A.T.) traveled for weeks through a region where many skulls of wild yaks were seen, reminiscent of the buffalo skulls in the early days of the American west.

The wild yaks are generally larger than domestic yaks and stand as high as six, possibly seven feet at the shoulder. Schafer[20] gives the height at withers of males as 200 cm. He states that sex dimorphism is very striking, bulls weigh-

ing up to 1,000 kg. and cows only about 300 kg. Such marked differences between the sexes are not found in domestic yaks. Schafer states that cows and calves often formed large herds, up to 2,000 head; these sometimes included young males while old males lived singly or in small groups. The horns of wild yaks are heavier and have a greater spread than those of domestic yaks. The wild yak is very cautious and will attack when cornered.

Some Tibetans claim that wild and domestic yaks cross occasionally. The crossbreeds are said to be larger and more difficult to handle, but can do more work and are hardier than the domestic type.

Conclusion

The yak has an important place in the economy of peoples living in the high plateau and mountainous regions of central Asia. Little attention has been given to improving the productivity of yaks through the application of modern knowledge of animal breeding, and much progress could no doubt be made in this way.

The hybrids between yaks and native cattle are useful utility animals, being superior to both parent types in many respects. It appears that even more useful hybrids can be provided through the use of superior domestic bulls of breeds such as the Brown Swiss. The effective utilization of hybrid females presents a difficult problem since natural mating is almost universal. Careful experimental work is needed to determine the best methods of utilizing these hybrid females, and this information should then be used as a basis for developing improved breeding methods among the native animals.

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✦

MUTATION MINK VARIETIES

A Correction

It is to be regretted that in a recent paper on the mutations of mink by Castle and Moore (vol. 37, p. 137) an earlier paper on the same subject by Smith *et al* (JOUR HERED. 32, May 1941) was entirely and inexcusably overlooked.

In both papers the same three mink mutations are described but with differences in names and genetic symbols which make correlation of the two reports difficult. This note is an attempt to remove that difficulty.

Popular names of mink varieties are frequently changed in the course of their exploitation and this makes their identification difficult in some instances such as the present. Genetic symbols, however, should be kept stable and here the rule of priority should hold. So the symbols used by Smith *et al* should prevail. Smith *et al* described under its original name, platinum, a recessive mutation to which Castle and Moore applied a substitute popular name, silverblu, recommended by the Mutation Mink Breeders' Association. Smith *et al* used for this mutation the symbol *p* for platinum, whereas we used the symbol *sb* for silverblu. Under the priority rule only *p* is the valid symbol for this mutation, whether it be popularly called either platinum or silverblu.

Smith *et al* also described and figured a dominant mutation silver, symbol *s*. This came to be known later by the popular name silver sable and, more recently, blufrost. Castle and Moore employed the latter two names with a symbol *F* for blufrost. Of course *S* is the valid symbol for the mutation, under whichever of its three popular names it is described. We have pointed out the probability that this mutation is lethal when homozygous, and this interpretation is supported by the findings of Smith *et al*, who report a population of 32 silvers : 16 normals produced by mating silver to silver. This is a perfect 2:1 ratio, which is expected to result where a gene is lethal when homozygous.

The third mutation reported by Smith *et al* is called blond or pastel both by him and by us, and the same symbol *b* is used by both, but for different reasons, as an abbreviation of blond by Smith *et al*, as an abbreviation of brown recessive allele of black by us. Fortunately no change is necessary in the terminology used in this case either of popular names or of symbols.

But in the case of another recessive mutation described by Castle and Moore, a change of symbols is desirable. A mutation discovered by F. R. Marsh of Portland, Oregon, was named by him imperial platinum in distinction from ordinary platinum or silverblu, which it resembles but from which it is genetically distinct since crosses of the two types produce normal dark animals. Because the use of the symbol *p* for platinum (silverblu) precludes its use for imperial platinum, as we had proposed, the symbol *ip* is suggested for the latter.

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FIRST AND SECOND GENERATION HYBRIDS OF LANDRACE AND DUROC-JERSEY

Figure 9

(Legend on page 217)

INHERITANCE OF COAT COLOR IN SWINE

V. Results of Landrace by Duroc-Jersey Crosses

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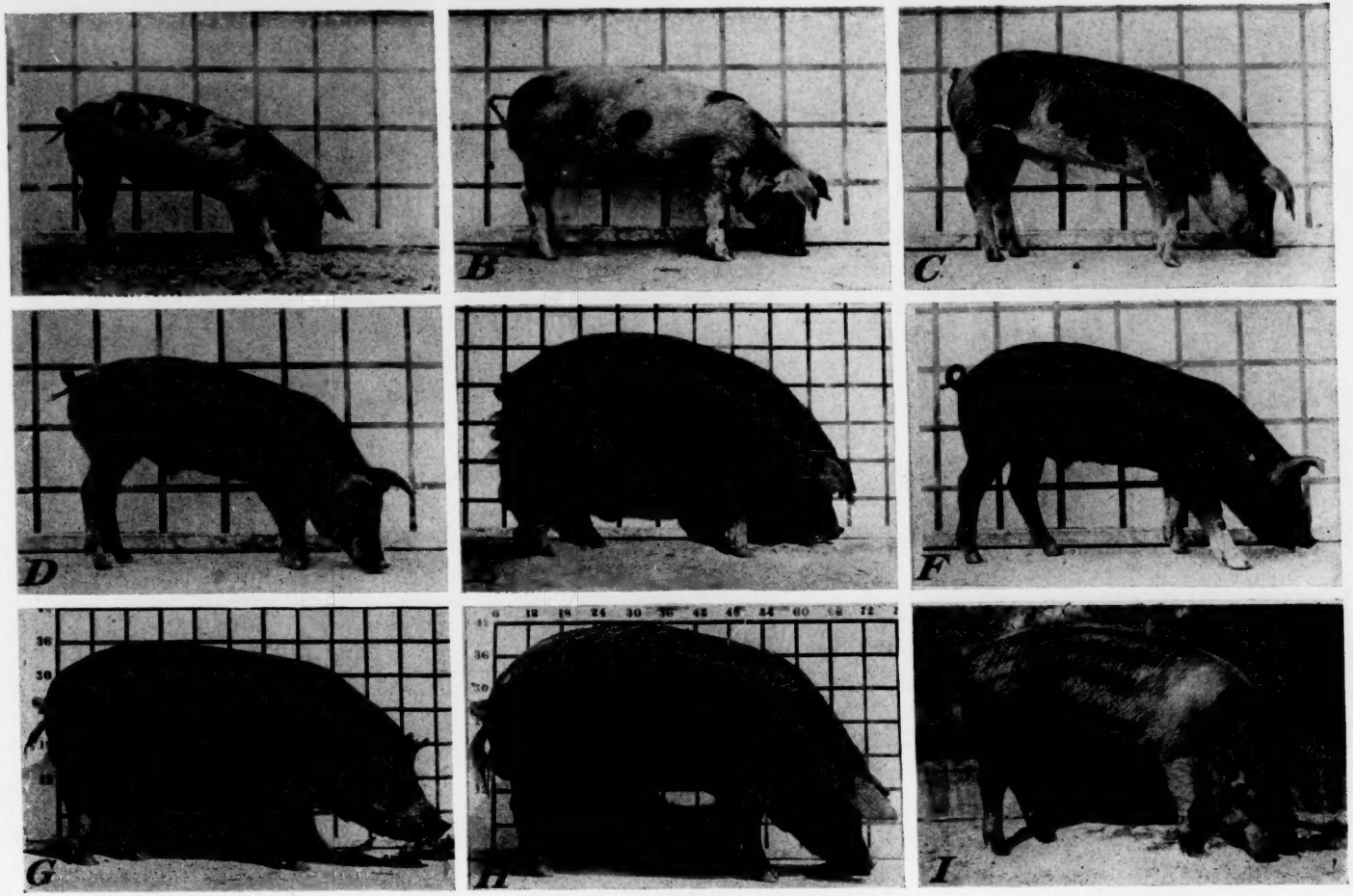
THE preceding papers of this series presented the author's findings with regard to color inheritance in crosses of the White Landrace pig with the Poland China, Berkshire and Large Black breeds[2,3,4]. The results could be explained by the action of two gene loci, *I* and *E*. The Landrace is homozygous for *I*, an inhibitor acting epistatically on the two alleles, *E* for complete extension of black, and E^p for partial extension of black. The recessive allele *i* permits the extension genes to manifest themselves. The basic genes conditioning coat color were thus E^pE^pII for the Landrace, E^pE^pii for the Poland China and Berkshire, and *EEii* for the Large Black. In addition the Landrace evidently has minor genes for restriction of black, while the other three breeds studied have minor genes for extension of black. The Landrace also appears to possess genes for dilution of red, lacking wholly or partially in the other three breeds.

The experiments to identify the color factors differentiating the Landrace from the Duroc-Jersey were begun by mating five Duroc-Jersey boars with 18 Landrace sows and one Landrace boar with two Duroc-Jersey sows. Later 19 Landrace (14 boars, 5 sows) and two Duroc-Jersey boars were used for backcrossing. All the Duroc-Jerseys were derived from registered stock purchased from different breeders. Their color was typical of the breed, being a medium red on a gray skin. The Landrace animals, some of which also were used in experimental crosses with the Poland China, Berkshire or Large Black, were all white or white with a few skin spots.

The 218 pigs obtained in the F_1 generation were all white or white with varying numbers of skin spots. They were similar to the F_1's from the Landrace × Poland China, Landrace × Berkshire and Landrace × Large Black crosses described previously, except that many had a distinct reddish tint over the dorsal parts of the body. Some also had longitudinal stripes, but as in the case of the Landrace × Large Black F_1's, the striping was not always distinct enough to permit further analysis (see Figure 9).

Of 22 F_1 sows ten were mated to three of the F_1 boars to produce a total of 300 F_2 pigs. In addition, 17 of the 22 sows produced a total of 209 backcross pigs by five Duroc-Jersey boars. The 300 F_2 pigs fall into six more or less distinct classes, namely 225 whites, 15 reds and 60 which were distributed among four new types as follows: 8 sandies, 2 black-spotted whites, 23 black-spotted sandies and 27 black-spotted reds. All these types except the black-spotted white class also occurred among the backcross pigs in the following distribution: 103 whites, 51 reds, 10 sandies, 13 black-spotted sandies and 32 black-spotted reds. For convenience in analysis these data will be considered under the following headings: I. Inheritance of white as opposed to colored or non-white; II. Inheritance of black spot-

←■ (Figure 9) *A*—Boar 94, one of the seven Duroc-Jersey boars used in the experiment. *B*—Sow 67, a Danish Landrace imported by the U. S. Department of Agriculture in 1934. *C* and *D*—F_1 litter mates out of sow 67 by boar 94, illustrating the variation in skin spotting among white individuals. *E*—A backcross sow out of F_1 67.4 (shown in *D*) by boar 94. The hair coat on this sow was white with a distinct reddish tint at birth. *F*—Another backcross sow sired by boar 94. Note uniformly red hair coat with lighter colored legs. *G*—An F_2 boar showing a darker shade of red with white belly. *H*—A sandy colored F_2 sow. *I*—An F_2 sow with black spots on a medium red background.



TYPES IN LATER GENERATIONS

Figure 10

ting; III. Inheritance of variations in intensity of red color.

Inheritance of White *vs* Colored

Table I shows the F_2 and backcross pigs classified as either white or colored. The F_2 distribution of 225 white, 75 colored is in perfect agreement with expectation on the basis of a 3:1 ratio; that observed in the backcross generation (103 white, 106 colored) closely approximates the expected 1:1 ratio. Evidently in this cross as in those reported earlier the dominant *I* gene of the Landrace inhibits the production of either black or red color. It is assumed that the recessive allele, *i*, is the same in the Duroc-Jersey as in the other breeds studied.

Additional data on the relations of white (*I*) to colored (*i*) are presented in the lower part of Table I, which includes a record of all other matings made in accordance with the plan of the experiment as outlined in an earlier paper.[1] Of the 1,960 pigs obtained from these matings, 525 were produced by crossing colored segregates of the F_2 and backcross generations (as well as of later segregating generations) back to the Landrace (topcross pigs); 358 were produced by interbreeding topcross animals (F_2-equivalent pigs); 472 were produced by backcrossing colored segregates to topcross animals (backcross-equivalent pigs); and 605 were produced by intercrossing colored segregates. The colored segregates in each case comprised varying numbers of reds, sandies, black-spotted sandies and black-spotted reds.

All except the backcross-equivalent pigs gave results consistent with those obtained in the F_1, F_2 and backcross

TABLE I. Relation of white to colored in the F_2 and backcross generations of the Landrace × Duroc-Jersey cross. Included are the results of all other matings made during the later stages of the experiment.

Name of crosses	Number of pigs			X^2	*P*
	Total	White	Colored		
F_2 generation					
F_1 white × F_1 white	300	225	75		
Expected (3:1)		225.0	75.0	0.0	1.0
Backcross generation					
Duroc-Jersey × F_1 white	209	103	106		
Expected (1:1)		104.5	104.5	0.04	0.84
*Topcross generation**					
Landrace × colored	525	525	....		
Expected (all white)		525.0	....	....	....
F_2-equivalent generation					
(L × colored) white × (L × colored) white	358	275	83		
Expected (3:1)		268.5	89.5	0.63	0.44
*Backcross-equivalent generation**					
(L × colored) white × colored	472	266	206		
Expected (1:1)		236.0	236.0	7.63	<0.01
Colored × colored	605	605			
Expected (all colored)		605.0	....	....	....

* Crosses made reciprocally.

←■ (Figure 10) *A-F*—Illustrating the diversity in size and distribution of black spots on animals with various type ground colors. Pigs in *A* and *B* were white with black spots when born. Pigs in *C* and *D* were sandy at birth, red roan when mature. Their sire, a medium red boar with black spots and white feet, is shown in *E*. Pig in *F* shows an unusually deep shade of red with white feet. *G*—A medium red boar with a sandy belly and sandy-tipped hairs. *H*—Boar, medium red with a few black spots. When mated to a white sow heterozygous for both the white gene *I* and the black spotted gene *Ep*, he produced 27 pigs, 11 of which were white or nearly white, 10 red with black spots, 4 sandy with black spots and 2 red roan with longitudinal stripes and a Hampshire-like belt. The two latter pigs, one of which is shown in *I*, are the only pigs whose identity with respect to the *I-i* pair of alleles remained doubtful. However, the fact that they resembled more nearly some heterozygous whites (*I-i*) than any of the other color varieties makes it probable that they were *Ii*, their red roan appearance being due to an unusually large number of modifying genes.

generations. The backcross-equivalent pigs, on the other hand, show a highly significant excess of the white class (exhibited about equally by males and females). This might be explained by an hypothesis that there is more than one kind of white, a possibility suggested by the variations in red color to be described later. Such an explanation seems improbable when we consider the fact that the F_2, backcross, and F_2-equivalent distributions all closely conformed to expectation on the basis of a single gene difference between white and colored. Furthermore, in only a few cases was there any difficulty in distinguishing white from any of the other color varieties. It may be concluded, therefore, that the poor fit exhibited by the backcross-equivalent pigs was not due to errors of classification.

Inheritance of Black Spotting

The occurrence of black-spotted and non-black sandies and reds among the F_2 and backcross pigs not only proves that the white of the Landrace is epistatic to both black and red color but also suggests that the absence of black in the Duroc-Jersey is determined by a recessive allele of the black spotting gene E^p previously demonstrated in the Landrace. The results expected on this theory, together with the numbers expected on the hypothesis that the alleles for black (E^p) and non-black (e) are inherited independently of the I, i pair of alleles, are shown in Table II. The table includes all matings summarized in Table I except for certain cases involving F_2, backcross and later generation hybrids. As some of the topcross animals having black-spotted parents may have been homozygous for the black-spotting pattern, it has seemed best to exclude from Table II all F_2-and backcross-equivalent pigs which traced to black-spotted animals. All topcross pigs were omitted. The results of the colored × colored matings which involved black-spotted animals, on the other hand, are based on the records of only such black-spotted animals as were known to have a non-black (i.e. sandy or red) parent or which proved capable of transmitting non-black. Thus, the F_2- and backcross-equivalent groups in Table II came from only such matings as were expected to give results similar to those obtained in the F_2 and backcross generations. The colored × colored matings are of three types as follows: a) heterozygous black

TABLE II. Data from Table I showing the colored class separated into black carriers and non-blacks.*

Name of crosses	Number of pigs				X^2	P
	Total	White	Colored			
			Black	Non-black		
F_2 generation						
F_1 white × F_1 white	300	225	52	23		
Expected (3:1)			56.2	18.8	1.28	0.26
Expected (12:3:1)		225.0	56.2	18.8	1.28	0.53
Backcross generation						
Duroc-Jersey × F_1 white	209	103	45	61		
Expected (1:1)			53.0	53.0	2.42	0.13
Expected (2:1:1)		104.5	52.2	52.2	2.49	0.29
F_2-equivalent generation						
(L × non-black) white × (L × non-black) white	144	113	25	6		
Expected (3:1)			23.2	7.8	0.53	0.48
Expected (12:3:1)		108.0	27.0	9.0	1.38	0.50
Backcross-equivalent generation						
(L × non-black) white × non-black	200	120	47	33		
Expected (1:1)			40.0	40.0	2.45	0.12
Expected (2:1:1)		100	50.0	50.0	9.96	<0.01
Colored × colored						
Black-spotted × black-spotted	109		86	23		
Expected (3:1)			81.8	27.2	0.88	0.36
Black-spotted × non-black	77		40	37		
Expected (1:1)			38.5	38.5	0.12	0.74
Non-black × non-black	30			30		
Expected (all non-black)				30.0	....	....

*See text above for reasons numbers do not add up to same totals as those shown in Table I.

× heterozygous black; b) heterozygous black × non-black; c) non-black × non-black.

Examination of the data in Table II shows that the F_2 consisted of 225 whites, 52 blacks (2 black-spotted whites, 23 black-spotted sandies, 27 black-spotted reds), and 23 non-blacks (8 sandies, 15 reds). This ratio closely approximates the expected 12:3:1 ratio ($\chi^2 = 1.28$, $P = 0.53$). Backcrossing F_1 to Duroc-Jersey resulted in 103 whites, 45 blacks (13 black-spotted sandies, 32 black-spotted reds) and 61 non-blacks (10 sandies, 51 reds), a ratio fairly close to the 2:1:1 ratio ($\chi^2 = 2.49$, $P = 0.29$). The results thus are consistent with the interpretation that the difference between black spotting and non-black is conditioned by the E^p-e alleles, inherited independently of I-i. The Duroc-Jersey lacks the black-spotting gene E^p and its genotype is ee ii as concerns these major pairs of genes.

The distribution in the F_2-equivalent group is in good agreement with the expected 12:3:1. The backcross-equivalent data, on the other hand, depart rather seriously from the expected 2:1:1 ratio ($\chi^2 = 9.96$, $P = < 0.01$). They show a considerable excess of the white class at the expense of both the blacks and non-blacks. As there was a similar excess of whites among the backcross-equivalent pigs tracing to black-spotted animals, it is clear that the same conditions probably caused these deviations in both groups. As regards the colored × colored matings in Table II, it will be seen that all of them gave results in close accord with their respective expectancies. They confirm the conclusion that the presence or absence of black depends on the E^p-e alleles.

It is worth noting (Table II) that except for three F_2 pigs (and a few pigs obtained in later generations) all pigs classed as black had black spots similar to those among the black-spotted Landrace × Poland China, Landrace × Berkshire or Landrace × Large Black hybrids described earlier. Our observations indicate, however, that the spots tended to be smaller than in the other crosses, and they tended to be more irregular in outline (see Figures 9 and 10). They also showed a greater amount of variation as regards the number of black spots present. Thus, a few pigs had only a single spot; others had as many as 70 or 80. The three exceptional F_2 pigs referred to above all had a number of black skin spots without any trace of black hairs, the hairs being some shade of sandy or red all over the body. Unfortunately it was not possible to determine the genetic constitution of these pigs. However, when we consider that animals known to be homozygous for black spotting occasionally produce offspring lacking any black hairs, it is probable that minor factors for restriction of black may cause genetically black-spotted pigs to be devoid of black pigment. This consideration seemed to justify the inclusion of the three exceptional F_2 pigs with those that were typically black-spotted. It might be added that none of the pigs classed as non-black had any trace of black pigment.

TABLE III. Distribution of color varieties in the F_2 and backcross generations together with numbers expected on hypothesis that presence of black is independent of variations in the red series.* Expected numbers are given in parentheses.

Presence or absence of black	Number of pigs			X^2	P
	White	Sandy	Red		
F_2 generation					
Black	2 (1.4)	23 (21.5)	27 (29.1)		
No black	(0.6)	8 (9.5)	15 (12.9)		
Total		31	42	1.73	0.43
Backcross generation					
Black	.. (....)	13 (9.8)	32 (35.2)		
No black	.. (....)	10 (13.2)	51 (47.8)		
Total	..	23	83	2.38	0.13

*Self-whites are omitted for reasons given in text.

The above results do not make it possible to predict the behavior of the red of the Duroc-Jersey toward the black of either the Poland China, of the Berkshire or of the Large Black. We may note that in the crosses involving the Large Black and the Landrace, black spotting was a simple recessive to self-black whereas in this cross it behaved as a simple dominant to self-red. The results, therefore, suggest that complete extension of black (E) as seen in the Large Black, partial extension of black (E^p) as seen in the Poland China and Berkshire, and complete restriction of black (e) as found in the Duroc-Jersey form a series of triple alleles with dominance in that order. The fact that both E (in the Landrace × Large Black cross) and e (in the cross reported here) were found to show no linkage with the dominant gene for white (I) supports this suggestion.

Inheritance of Variations in Intensity of Red

If the F_2 and backcross generation whites are omitted on the theory that self-white is epistatic to both black and red color, the results shown in Table III are obtained. When we consider that sandy and red occurred in both the presence and absence of black and that two of the black-spotted F_2 pigs had a white rather than a sandy or a red background, it may be assumed that the Landrace is capable of transmitting two genetically distinct kinds of white and that the white in combination with black represents a dilute form of red in which sandy occupies an intermediate position. Before proceeding, it is important, therefore, to determine whether any of the self-whites owed their appearance to a dilution of red. While this question cannot be answered with certainty, it is worth noting that when the data in Table III are tested against the numbers expected on the hypothesis that the presence of black is independent of variations in intensity of red, the probabilities of obtaining as great deviations by random sampling are 0.43 and 0.13 for the F_2 and backcross pigs, respectively. These findings, together with the fact that the expected number of whites was only about 0.6 in the F_2 and zero in the backcross generation, make it probable that none of the F_2 or backcross generation whites were dilute reds and that the inheritance of the E^p-e pair of alleles is independent of those primarily responsible for variations in the red series.

A point of considerable interest in this connection is that no correlation was evident between intensity of red and extent of black among either the F_2 or backcross pigs. These results are somewhat different from those obtained by other workers, notably Wentworth and Lush[5] who observed a negative correlation between intensity of red and extent of black. This difference might be due to the fact that the amounts of black

TABLE IV. Distribution of color varieties in F_2 and backcross generations with numbers expected under various hypotheses. Ratios used to calculate expected numbers are given in parentheses.*

Color of pigs	Number of pigs	Numbers expected on the hypothesis that red is due to: one main gene	two dominant genes	two partially dominant genes	three partially dominant genes	two partially recessive genes	three partially recessive genes
F_2 generation							
White	2	18.8 (1)	4.7 (1)	4.7 (1)	1.2 (1)	4.7 (1)	1.2 (1)
Sandy	31	37.5 (2)	28.1 (6)	46.9 (10)	51.6 (44)	37.5 (8)	30.4 (26)
Red	42	18.8 (1)	42.2 (9)	23.4 (5)	22.2 (19)	32.8 (7)	43.4 (37)
X^2		44.92	1.84	21.57	26.17	5.24	0.64
P		<0.01	0.41	<0.01	<0.01	0.07	0.73
Backcross generation							
Sandy	23	53.0 (1)	.....	26.5 (1)	13.2 (1)	26.5 (1)	13.2 (1)
Red	83	53.0 (1)	106.0	79.5 (3)	92.8 (7)	79.5 (3)	92.8 (7)
X^2		33.96	.....	0.62	8.20	0.62	8.20
P		<0.01	.....	0.45	<0.01	0.45	<0.01

*Reasons for omitting self whites and for disregarding presence of black spots are given in text.

on the pigs of this experiment seldom exceeded more than one-third of the body surface, whereas somewhat larger amounts were observed by the above workers.

In view of the above findings, it is legitimate to omit all self-whites and to disregard the presence of black for the remainder of the analysis. However, before proceeding it will be well to note briefly the differences in appearance between the white, sandy and red classes.

While there was never any question about the classification into white and red, it was difficult in some cases to distinguish accurately between white and sandy and between sandy and red. Consequently it became necessary to draw a somewhat arbitrary line in classifying some animals. Another point of considerable interest is that many of the sandy and red colored pigs had white feet, white or sandy bellies, a white patch on the forehead or a few irregularly shaped patches of white over other parts of the body. Others in turn had a distinct roaning pattern of sandy and white hairs or of red sandy and white hairs. Whatever the nature of these patterns, they will not be considered further in this discussion. It might be said that while the white in pigs with black spots appeared to be a pure white at birth, it always turned into a yellowish white on a gray skin, whereas no such change was observed among any of the self-whites. Some of the sandy and red pigs, on the other hand, became lighter as they matured, although a few became darker. Curiously enough the most striking changes occurred among the reds a few of which, when mature, were a dark reddish brown. As not all pigs were kept to maturity, the color records used here are those at time of birth.

In spite of the difficulties outlined above, the use of the terms white, sandy and red probably provides the most reliable means of distinguishing between the different intensities of red. Not only could most of the pigs readily be assigned to one of these groups, but such evidence as the writer has suggests that differences in minor genes were responsible for most of the doubtful cases.

The hypotheses which might reasonably be examined in this connection are: (1) that red and white are differentiated by one major gene, the heterozygous condition resulting in sandy; (2) that there are two dominant genes each of which by itself gives sandy while the absence of both results in white; (3) that there are two or three genes with red partially dominant to sandy and white; (4) that white and sandy are dilute forms of red, the concurrence of two or three partially dominant genes being necessary to dilute red to sandy or white. The results obtained in the F_2 and backcross generations with the distributions expected under the various hypotheses are given in Table IV.

That the differences in intensity of red cannot be due to only one major gene is clearly shown by the fact that both the F_2 and backcross distributions differ significantly from those expected on that basis. Nor do the data conform to the hypothesis that red is due to the action of two dominant genes, as Wentworth and Lush[5] suggested to explain the results of their Berkshire $\times$ Duroc-Jersey crosses. This hypothesis is adequate to account for the F_2 distribution observed in our data, but it would preclude the occurrence of sandies in the backcross generation. The assumption that red depends on two partially dominant genes adequately accounts for the distribution observed in the backcross generation, but does not conform even approximately to the F_2 data. The results are even more difficult to explain on the assumption that there are three partially dominant genes for red. It is clear that hypotheses (1), (2), and (3) do not adequately account for the observed data.

It remains to be shown, therefore, that the results are in agreement with those expected on the hypothesis of partially dominant dilution genes. The F_2 frequencies are only moderately close to the expected on the basis of two genes, but are in excellent agreement with expectation on the basis

of three genes. The backcross results, on the other hand, depart rather seriously from expectation on the basis of three genes, but are in good accord with segregation of two genes. While these results might warrant the formulation of another hypothesis, any such attempt is obviously futile unless it could be tested by further key matings. In the absence of such tests, we may tentatively conclude that there are two partially dominant dilution genes, for as noted above neither did the F_2 nor the backcross generation give results significantly different from the expected. It is also possible, however, that some of the parental animals carried certain modifying genes not present in others and that there are three genes of comparable importance. The genotype of the Landrace may thus be tentatively formulated as $E^p\ E^p\ I\ I\ D_1\ D_1\ D_2\ D_2$—and that of the Duroc-Jersey as $e\ e\ i\ i\ d_1\ d_1\ d_2\ d_2$—, where $D_1\ d_1$ and $D_2\ d_2$ represent some set of genes with white (dilute red) partially dominant to sandy and sandy partially dominant to red.

Since the F_2-and backcross-equivalent data proved of little value in investigating further the inheritance of shades of red, the only other data to be discussed here are those from the colored × colored matings. They were of three types as follows: (a) sandy × sandy; (b) sandy × red; and (c) red × red. While none of the animals could be assigned a specific formula on either its appearance or progeny record, it is worth noting that the results of the sandy × sandy matings could readily be explained on the basis of either two or three genes with white at least partially dominant. This statement also applies to the sandy × red and the red × red matings except that both types produced a few white pigs where none was expected. Their occurrence is no more satisfactorily explained by any of the other hypotheses referred to above. Since the various classes graded into each other, it is possible that differences in minor genes for dilution of red account for the exceptional pigs.

Summary

An analysis of the color factors differentiating the Landrace and Duroc-Jersey is reported.* Like the Poland China, Berkshire and Large Black, the Duroc-Jersey owes its color primarily to the gene *i*, whose dominant allele *I* carried by the Landrace is epistatic to both black and red color.

The occurrence of black-spotted pigs in both the F_2 and backcross generations confirms the conclusion drawn earlier that the Landrace carries the same gene E^p for partial extension of black as do the Poland China and Berkshire. This gene behaves as a dominant to the absence of black in the Duroc-Jersey, indicating that complete extension of black (E), as seen in the Large Black, partial extension of black (E^p) as seen in the Poland China and Berkshire, and complete restriction of black (e), as manifested by the absence of black in the Duroc-Jersey, form a series of triple alleles.

The data give no indication of linkage between E^p and I.

Evidence for the existence of a white which is genetically different from that due to the inhibitor I was furnished by the fact that a few pigs showing black spots on a white body color were recorded in the F_2 generation. This white is considered to represent a dilute form of red with sandy as an intermediate variation.

There appear to be no clear-cut genetic factors for the differences between white, sandy and red. However, there is evidence for the existence of two or three major dilution genes with white partially dominant to sandy and sandy partially dominant to red.

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*Data obtained at the Agricultural Research Center, Beltsville, Md. The author acknowledges his indebtedness to Mr. J. X. King for recording the colors of the pigs used in this study.

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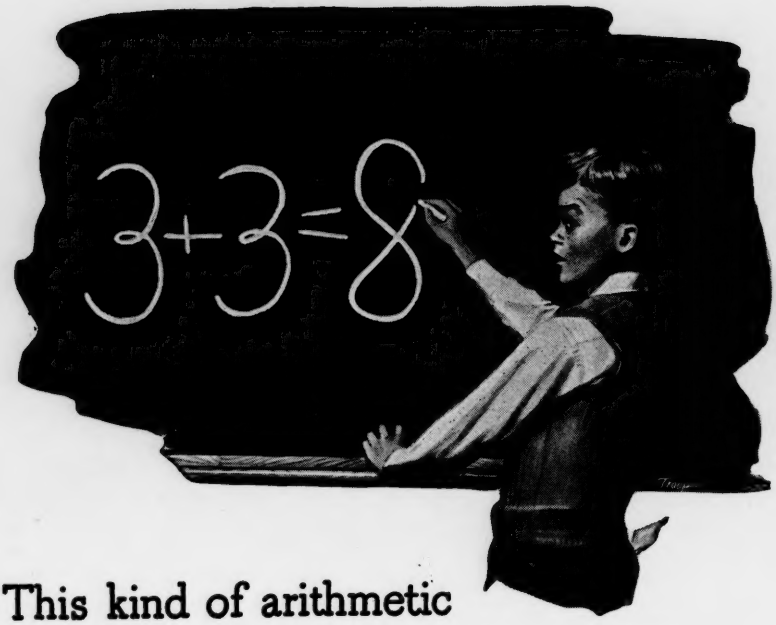

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